



Anthropogenic nitrogen deposition alters growth responses of European beech (*Fagus sylvatica* L.) to climate change[☆]



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ABSTRACT

Global change affects the functioning of forest ecosystems and the services they provide, but little is known about the interactive effects of co-occurring global change drivers on important functions such as tree growth and vitality. In the present study we quantified the interactive (i.e. synergistic or antagonistic) effects of atmospheric nitrogen (N) deposition and climatic variables (temperature, precipitation) on tree growth (in terms of tree-ring width, TRW), taking forest ecosystems with European beech (*Fagus sylvatica* L.) as an example. We hypothesised that (i) N deposition and climatic variables can evoke non-additive responses of the radial increment of beech trees, and (ii) N loads have the potential to strengthen the trees' sensitivity to climate change. In young stands, we found a synergistic positive effect of N deposition and annual mean temperature on TRW, possibly linked to the alleviation of an N shortage in young stands. In mature stands, however, high N deposition significantly increased the trees' sensitivity to increasing annual mean temperatures (antagonistic effect on TRW), possibly due to increased fine root dieback, decreasing mycorrhizal colonization or shifts in biomass allocation patterns (above-ground vs. belowground). Accordingly, N deposition and climatic variables caused both synergistic and antagonistic effects on the radial increment of beech trees, depending on tree age and stand characteristics. Hence, the nature of interactions could mediate the long-term effects of global change drivers (including N deposition) on forest carbon sequestration. In conclusion, our findings illustrate that interaction processes between climatic variables and N deposition are complex and have the potential to impair growth and performance of European beech. This in turn emphasises the importance of multiple-factor studies to foster an integrated understanding and models aiming at improved projections of tree growth responses to co-occurring drivers of global change.

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1. Introduction

Global change drivers such as climate change and atmospheric nitrogen (N) deposition trigger biodiversity loss and impair ecosystem functions on regional and global scales (Sala et al., 2000; Calvo-Fernandez et al., 2017). Climate change affects ecosystem functions such as primary productivity, nutrient cycles, and the

complex interplays within and between species (Law, 2013; Hölzel et al., 2016). Anthropogenic N emissions have contributed to rising ecosystem nutrient levels, accompanied by shifts in N cycles and losses in species diversity (Gruber and Galloway, 2008; Bobbink et al., 2010; De Schrijver et al., 2011).

These changes in the Earth system are not just co-occurring but also are causally linked (Zavaleta et al., 2003), and interacting effects might have far-reaching implications for ecosystems and the services they provide (Greaver et al., 2016). As a consequence, an integrated understanding of the combined effects of climate and atmospheric changes on ecosystems is crucial for the guidance of management, mitigation efforts and biodiversity conservation.

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Important approaches to increase our understanding of ecosystem responses to atmospheric changes are multifactorial studies in which single and combined effects of driving variables are quantified. This data can further help to parameterise and evaluate models designed to predict shifts in ecosystem functions and services caused by global change (Dieleman et al., 2012). Although a bulk of recent work has focused on single effects of global change drivers on different ecosystem functions, we still lack an integrated understanding of how climate and atmospheric changes interactively may alter ecosystem processes in the course of this century (Dieleman et al., 2012; Greaver et al., 2016; Chelli et al., 2017). This regards the effects of climate change and N deposition in particular, because only few studies have quantified the interactive processes at the species or ecosystem level (Gaudnik et al., 2011; Law, 2013; Dzionek et al., 2017). The complexity and nature of global change interactions, in turn, may influence our ability to understand and anticipate ecosystem responses to environmental shifts.

In the context of global change research, the effects of climate and atmospheric changes on forest ecosystems are of particular interest. Forests provide important ecosystem services, play a crucial role in the global carbon (C) and N cycle, and are among the most important repositories of terrestrial biodiversity (Luyssaert et al., 2008; Peñuelas et al., 2008). Both airborne N loads and climate change (including interaction effects) can impair carbon uptake by trees and its sequestration in forest soils (Law, 2013). However, the long-term effects of N deposition on tree growth and forest carbon sequestration are still unclear and controversially debated (Magnani et al., 2007; De Schrijver et al., 2008; De Vries et al., 2008; Gruber and Galloway, 2008; Greaver et al., 2016). From a European perspective, forest ecosystems with European beech (*Fagus sylvatica* L.) are of particular importance from both an ecological and economic point of view (Ellenberg and Leuschner, 2010). In recent decades, European beech often showed increasing increment rates on the tree- and stand-level, mainly attributable to prolonged growing seasons, increasing atmospheric CO₂ levels, or improved N supply (Dittmar et al., 2003; Lebourgeois et al., 2005; Pretzsch et al., 2014). N deposition may also affect understorey species richness (e.g. increase of nitrophilous species), N cycling, mycorrhiza colonization, N leaching, and soil acidification (De Schrijver et al., 2008; Bobbink et al., 2010). European beech trees, however, are also considered sensitive to increasing summer temperature and drought events (Gessler et al., 2007; Friedrichs et al., 2009; Zimmermann et al., 2015), and thus may suffer from climate shifts as currently projected by climatic models (IPCC, 2013). The interactive effects of N deposition and climatic variables on growth rates of European beech have not been quantified yet, and it remains unclear whether N deposition and climate change additively or non-additively affect radial growth of *Fagus sylvatica*. It is, for example, conceivable that N deposition and climatic variables have non-additive effects on growth responses of European beech in that N deposition increases the trees' sensitivity to drought or increasing temperatures (Höglberg et al., 1993; Dzionek et al., 2017).

The overall objective of the present study was to illustrate that interactions of global change drivers may strongly influence both our understanding and predictions of tree growth responses to environmental shifts. Specifically we asked whether atmospheric N deposition can alter tree growth responses to climatic variables. To this end we quantified single and interaction effects of N deposition and climatic variables (temperature, precipitation) on tree growth (in terms of tree-ring width), taking forest ecosystems with European beech in the centre of its distribution range (Central Europe, Luxembourg) as an example. We compared stands of different age (young and mature stands) to additionally assess age-related

effects on tree growth responses (Luo and Chen, 2013). Based on model predictions, we used contour plots to visualise present and future responses of tree growth to possible shifts in climate and N deposition. We hypothesised that (i) N deposition and climatic variables might evoke non-additive responses of the radial increment of European beech, and (ii) N deposition has the potential to increase the trees' sensitivity to climate shifts.

2. Materials and methods

2.1. Study area and forest site selection

Our study area was located in Central Europe (Luxembourg; N 49°45'–49°51' and E 6°18'–6°24'; 255–420 m above sea level; Fig. 1) and spanned an area of about 180 km². The climate is of a sub-oceanic type (i.e. mild winters, humid summers). Precipitation is 750–800 mm yr⁻¹ and the annual mean temperature is 8–9 °C (Pfister, 2005). Soils in the study area developed from Jura-Sandstone, and the forests analysed were grown on Regosols with transitions to Leptosols (Krippel, 2005).

Forests cover about 35% of the total study area, and we selected a total of eight forest sites (respectively four young and mature forests) representing acidophytic beech forest ecosystems typical of the study area (Luzulo-Fagetum sensu Ellenberg and Leuschner, 2010). Forest sites were about 0.25 ha in size and embedded in discrete larger forests ranging in size from 0.5 to 5 km². Forests were separated mainly by pastures. Forest selection criteria were: upper canopy closure >80% in the upper canopy; *Fagus sylvatica* is the dominant tree species in the upper canopy (i.e. cover >80%); no admixture of non-native tree species; natural tree rejuvenation and near-natural dynamics; no major forestry operations during the last decade. Soil chemical properties of the forest sites analysed are presented in Table 1.

2.2. Tree selection and sampling design

In May 2008, each forest site was overlaid with a grid, and 10 intersections per site selected at random. The tallest (dominant) tree individuals of the upper canopy nearest to an intersection were considered for analyses (henceforth referred to as target trees; 10 trees per forest site; total no. of trees analysed: 80; distances between target trees were 10–70 m and 15–70 m in young and mature stands, respectively). Target trees were cored with an increment borer (Suunto 400, Vantaa, Finland), 40 cm in length and 0.5 cm in bit diameter. Two cores per tree were taken at 1.3 m height from two opposite sides.

2.3. Tree-ring analyses

Tree-ring analyses followed the procedure as described in Härdtle et al. (2013; i.e. drying, fixing, and levelling of the core's surface with a core-microtome (WSL Birmsdorf, Switzerland), then measurement of the tree-ring width (TRW) with a measuring table with 0.01 mm resolution (Instrumenta Mechanik Labor IML, Wiesloch, Germany)). All TRW series were cross-dated following the procedure described by Yamaguchi (1991), using chronologies of Friedrichs et al. (2009) as reference and the software TSAP-Win (Version 0.53, Rinntech, Heidelberg, Germany). The TRW series of the two cores per tree were averaged to tree mean curves and confined to the period 1983–2007 (coinciding with period for which data on N deposition were available for the study area; see description below).

To describe stand growth characteristics, we calculated stand basal area increment (BAI) and descriptive statistics on ring-width series (standard deviation (SD), first-order autocorrelation (AC),

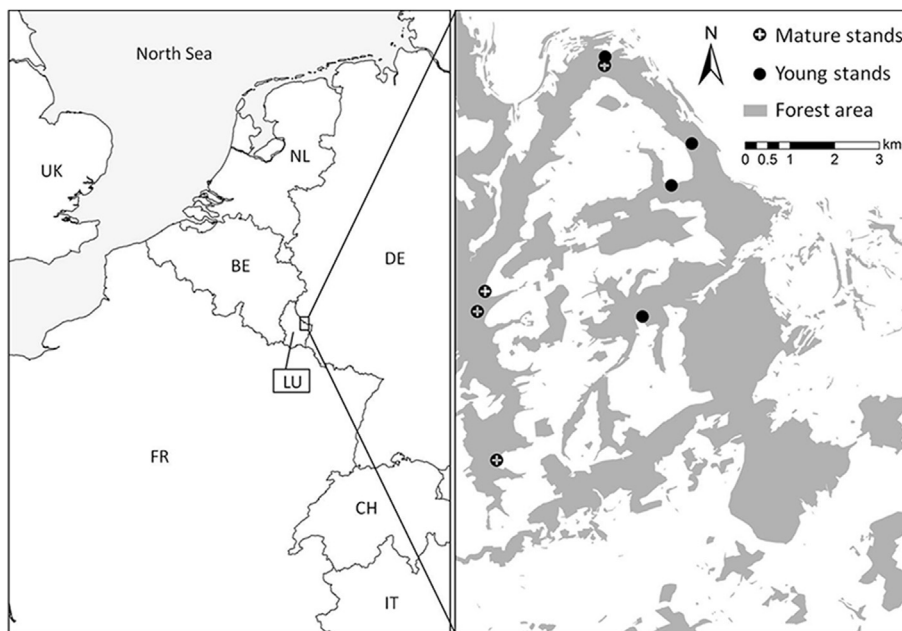


Fig. 1. Location of the study area (sandstone region) in Luxembourg.

Table 1

Stand and site description (means of four forest stands per type) and growth characteristics (25-years chronologies, means of four forest stands per type) of the *Fagus sylvatica* stands analysed. Abbreviations: DBH = diameter at breast height (1.3 m above ground), BA = basal area, TRW = tree-ring width, BAI = basal area increment, SD = standard deviation of TRW, AC = first order autocorrelation, MS = mean sensitivity. Different subscript letters indicate significant differences ($P < 0.05$; based on a Tukey post-hoc test). Data on soil characteristics were taken from Härdtle et al. (2013).

Stand characteristics	Mature stands	Young stands
Altitude a.s.l. (m)	341	335
Age of trees (years)	202	52
Tree density (DBH > 7 cm; n ha ⁻¹)	224	919
DBH (cm)	56	23
BA (m ² ha ⁻¹)	33.0	22.2
Stand volume (m ³ ha ⁻¹)	688	299
Soil characteristics (A-horizon)		
Soil pH (H ₂ O)	3.8	3.7
Base saturation (%)	43	55
CN-ratio	18.2	20.3
Growth characteristics		
TRW (0.01 mm yr ⁻¹)	148.6 ^a	284.2 ^b
BAI (cm ² yr ⁻¹)	24.6 ^a	14.3 ^b
SD (mm yr ⁻¹)	0.55 ^a	0.76 ^b
AC	0.38 ^a	0.56 ^b
MS (%)	30.3 ^a	17.1 ^b

and mean sensitivity (MS; mean percentage change from each measured yearly ring value to the next) using TSAP-Win.

For each tree-ring series, a tree-ring standardisation was performed (Cook and Peters, 1997; Fritts, 2001). To this end, the first-order auto-correlation in all tree-ring series was removed based on an autoregressive model (Cook and Kairiukstis, 1990; Pinheiro and Bates, 2000). Subsequently, tree-ring series were detrended by fitting an exponential trend line (Bunn, 2008) to remove age-related and other biological or non-climate related variations and noise. The standardised ring width indices (henceforth referred to as RWI) were used as a response variable in the mixed models (see below).

2.4. Meteorological and N deposition data

The radial increment of trees responds to a wide range of meteorological variables, but their predictor quality for TRW often is species- and site-specific. In the present study we were not interested in general TRW-climate relationships, but in interactive effects between important climatic predictors for TRW and N deposition. Therefore, we surveyed the dendroecological literature to detect the most important climatic predictors for TRW of *Fagus sylvatica* (preferably with regard to our study sites and adjacent areas). In this literature survey, annual mean temperature (T_{mean}) and growing season precipitation (P_{gs} ; i.e. precipitation from April to October) of the year of tree-ring formation proved to be the best climatic predictors of TRW for the tree species considered (cf. Dittmar et al., 2003; Friedrichs et al., 2009; Härdtle et al., 2013). We thus focused on these climatic variables to (exemplarily) quantify how they interact with N deposition on radial increment. Data for T_{mean} and P_{gs} of study area were obtained from Freyer-muth and Pfister (2010). Data on annual total atmospheric N deposition (N_{tot} deposition = annual wet deposition and dry deposition for the period 1983–2007; calculated from monthly values) in the study area were taken from the European Monitoring and Evaluation Programme EMEP/CCC Report (Hjellbrekke and Fjæraa, 2010). For analyses, N deposition data and climatic variables were linearly detrended to remove the effects of long-term trends (Bachelet et al., 2001; Härdtle et al., 2013).

2.5. Data evaluation and statistical analysis

We applied linear mixed-effects models (LMM) to analyse the effects of N-deposition and climatic conditions on RWI. Forest site was used as random effect to account for variability between the forest sites. We also tested for spatial auto-correlation within the forest sites and the trees selected for analyses, but found no violation of independence according to a Moran's I test. N deposition, T_{mean} and P_{gs} and all two-way interactions between N deposition and climatic variables (T_{mean} , P_{gs}) were considered as fixed effects. Model selection (determination of the best-fitting and most

parsimonious model) was based on the Akaike information criterion (AIC) using maximum likelihood (ML) estimations and the model with the smallest AIC was chosen as the best-fitting model (Burnham and Anderson, 2002). Parameter estimates of the best-fitting models were based on the restricted maximum likelihood (REML) method.

Combined effects of N deposition and climatic variables (i.e. N deposition vs. T_{mean} , and N deposition vs. P_{gs}) on RWI were visualised by means of contour plots based on predicted values derived from LMM. To assess the potential effects of climate change and N deposition on RWI, contour plots also visualise currently projected shifts in T_{mean} and P_{gs} in the study area until the end of the 21st century. Climate change scenarios were based on a new set (up to January 2016) of future climate projections for Europe generated within the 'Coordinated Regional Downscaling Experiment' (CORDEX; Giorgi et al., 2009; Jacob et al., 2014). Regional climate models are dynamically downscaling CMIP5 global climate projections (Taylor et al., 2012), which are based on Representative Concentration Pathways (RCP) scenarios (Moss et al., 2010). Here, results from high resolution simulations (~12.5 km horizontal grid spacing) for RCP4.5 and RCP8.5 have been used to estimate changes in temperature and precipitation between the current climate and the projected climate at the end of the 21st century. RCP4.5 is an intermediate stabilisation pathway in which radiative forcing is stabilised at approximately 4.5 Wm^{-2} after 2100 through relatively ambitious emissions reductions. RCP8.5 is a high emission pathway for which radiative forcing reaches more than 8.5 Wm^{-2} by 2100; it is thus characterised by rising greenhouse gas emissions (Van Vuuren et al., 2011). The moderate RCP4.5 scenario corresponds to the B1 scenario of the older SRES (Nakićenović and Swart, 2000) scenario family, and the strong RCP8.5 compares to the SRES A1FI scenario (Quante and Bjørnæs, 2016). Projected climate shifts were expressed as median and range values of model projections (i.e. for study area-related shifts in T_{mean} and P_{gs}).

All statistical analyses were conducted in R 3.0.3 (<http://www.R-project.org>) with the packages lme4 (Bates et al., 2014) and lmerTest (Kuznetsova et al., 2014).

3. Results

3.1. Growth characteristics

TRW was higher in young than in mature stands, but mature stands showed a higher BAI (Table 1). SD of TRW and AC was higher for young than for mature stands. In contrast, young stands showed a lower MS than mature stands (17.1% vs. 30.3%, respectively).

3.2. Effects of N deposition and climatic variables

Mature and young stands showed different responses to shifts in climatic and atmospheric conditions. In mature stands, N deposition interacted with T_{mean} antagonistically: Increasing N deposition and T_{mean} significantly decreased RWI (non-additive effect; Table 2). Moreover, N deposition interacted with P_{gs} (negative estimate), but this interaction was only marginally significant ($P = 0.058$; Table 2).

In young stands, P_{gs} positively affected RWI (as a single factor), and N deposition and T_{mean} showed a marginally significant interaction effect on RWI (with a mutually amplifying effect on RWI). In contrast, interaction effects between N deposition and P_{gs} were not significant for young stands.

Additive and non-additive effects of N deposition and climatic variables on RWI were visualised by the contour plots in Fig. 2. In addition, the contour plots allow for an estimation of how RWI will respond to possible shifts in both N deposition and climatic

Table 2

Best-fitting mixed-effects models for ring width indices (RWI) of the radial increment of mature and young *Fagus sylvatica* as affected by annual nitrogen deposition (N), annual mean temperature (T_{mean}), and growing season precipitation (P_{gs}). Significant and marginally significant P -values in bold and underscored, respectively.

Fixed effects	Estimate	Std. error	d.f.	T value	P
Mature <i>Fagus sylvatica</i> stands					
Intercept	1.047	0.012	954	85.350	<0.001
N	−0.004	0.018	954	−0.241	0.810
T_{mean}	−0.012	0.013	954	−0.977	0.329
P_{gs}	0.035	0.013	954	2.697	0.007
N x T_{mean}	−0.099	0.012	954	−8.579	<0.001
N x P_{gs}	−0.024	0.013	954	−1.900	<u>0.058</u>
Young <i>Fagus sylvatica</i> stands					
Intercept	1.006	0.006	955	159.833	<0.001
N	<0.001	0.008	955	0.085	0.932
T_{mean}	0.069	0.007	955	9.850	<0.001
P_{gs}	0.036	0.008	955	4.802	<0.007
N x T_{mean}	0.012	0.006	955	1.917	<u>0.056</u>

variables (i.e. shifts in T_{mean} and P_{gs} according to the RCP scenarios considered; cf. horizontal dashed lines in Fig. 2 and figure legend).

Fig. 2 a) shows that shifts in RWI of mature stands are low for increasing T_{mean} under current N deposition rates (i.e. no effect of increasing T_{mean} under N deposition rates of about $9 \text{ kg ha}^{-1} \text{ yr}^{-1}$; also see Table 2). However, currently projected shifts in T_{mean} (for both RCP scenarios) may negatively affect RWI when co-occurring with increasing N deposition (e.g. N depositions rates $>12 \text{ kg N ha}^{-1} \text{ yr}^{-1}$; right part of the Fig. 2 a), indicating a non-additive interaction effect of T_{mean} and N deposition. Decreasing P_{gs} negatively affects RWI under low rates of N deposition ($<8 \text{ kg ha}^{-1} \text{ yr}^{-1}$; Fig. 2 b), but the negative effects of decreasing P_{gs} were compensated for under higher N deposition rates ($>10 \text{ kg ha}^{-1} \text{ yr}^{-1}$). Projected shifts in P_{gs} will hardly affect these response patterns.

For young stands, Fig. 2 c) visualises the mutually amplifying effects of increasing T_{mean} and N deposition on RWI (i.e. highest RWI values for high T_{mean} and N deposition rates). Increasing RWI is particularly pronounced under the RCP8.5 scenario and high N loads. In contrast, the positive effects of N deposition on RWI were hardly influenced by shifts in P_{gs} (Fig. 2 d); no significant interaction according to the LMM). Thus, RWI will hardly respond to projected shifts in P_{gs} (according to both RCP scenarios).

4. Discussion

Our findings support our first hypothesis that N deposition and climatic variables may provoke both synergistic and antagonistic effects on the radial increment of European beech. This applied to N deposition and T_{mean} in particular, which non-additively affected RWI of young and mature stands (if marginal effects are included). As a consequence, single factor analyses could lead to both under- and overestimation of tree growth responses to co-occurring global change drivers, given that their interactions are synergistic and antagonistic, respectively (Dieleman et al., 2012; Law, 2013). This in turn suggests that predictions of combined effects of atmospheric and climate changes on tree growth remain challenging (Greaver et al., 2016), since interactions may be both additive and non-additive, and also depend on the trees' age.

4.1. Interaction effects of N deposition and T_{mean}

High N deposition has the potential to significantly increase the trees' sensitivity to increasing temperatures (as currently predicted by the RCP scenario based projections). This was indicated by a highly significant interaction term for N deposition and T_{mean} for mature trees, and confirms our second hypothesis. Although

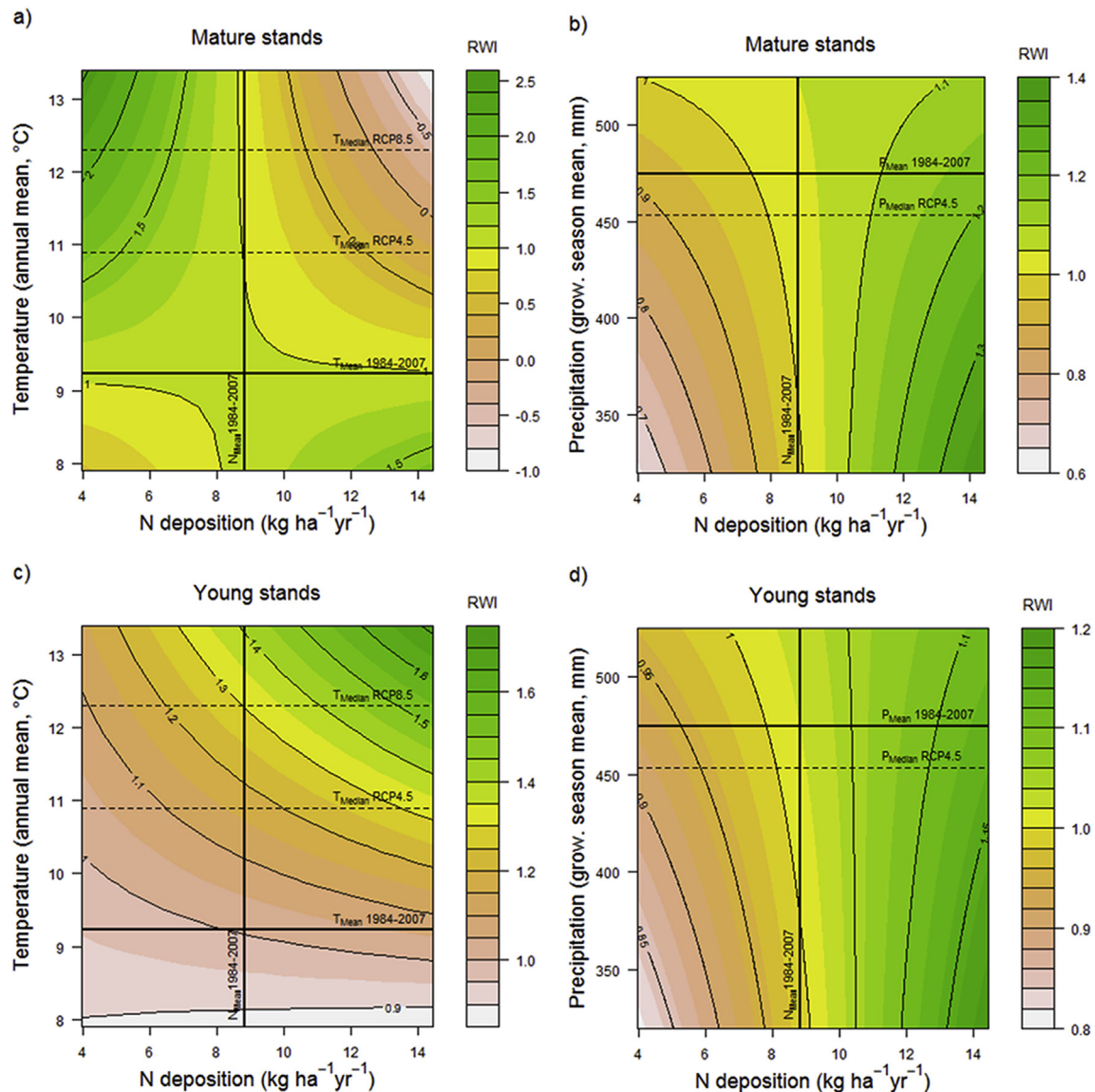


Fig. 2. Impact of global change drivers on radial increment of European beech. Contour plots illustrate the growth responses of *Fagus sylvatica* (in terms of standardised tree-ring width: RWI) to nitrogen (N) deposition and climatic variables (annual mean temperature (T_{mean}) and growing season precipitation (P_{gs})). RWI responses of a) mature stands to N deposition and T_{mean} ; b) mature stands to N deposition and P_{gs} ; c) young stands to N deposition and T_{mean} ; d) young stands to N deposition and P_{gs} . Solid lines indicate the current rates of total N deposition, T_{mean} and P_{gs} for the study area. Dashed lines indicate currently projected shifts in T_{mean} and P_{gs} according to Representative Concentration Pathways (RCP scenarios; Moss et al., 2010).

Explanation of model projections (RCP4.5 and RCP8.5) for shifts in T_{mean} and P_{gs} for the study area:

The median of annual mean surface air temperature changes for RCP4.5 is 1.7 °C (range: 1.4 °C–2.8 °C) and for RCP 8.5 is 3.1 °C (range: 2.6 °C–4.8 °C; dashed lines in Fig. 2) a) and c). All underlying simulations show a warming for all seasons, whereby the lowest warming is projected for the spring months.

The median of growing season precipitation changes for RCP4.5 is –4.5% (range: –11.8%–16.6%) and for RCP8.5 is –2.8% (range: –19.4%–14.1%; note: dashed lines in Fig. 2) b) and d) only depict the RCP4.5 scenario based projections). The signals of change are not uniform over the growing season, since almost all simulations reveal wetter spring months and dryer summer months. As a result, the decrease in projected changes over the entire growing season is relatively small due to mutual (i.e. dryer-wetter) compensations.

positive effects of airborne N loads on tree growth have been documented for N-limited forests (Rennenberg et al., 1998; Pretzsch, 1999; Nadelhoffer, 2000), there is also evidence for thresholds of N inputs above which growth rates remain unaltered or even decrease due to N surplus (Thomas et al., 2002) or nutrient imbalances (Fleischer et al., 2013). Antagonistic effects of increasing N inputs and T_{mean} could be attributable to several mechanisms: (i) N fertilisation affects biomass allocation patterns of plants according to the ‘resource optimisation hypothesis’ (Ågren and Franklin, 2003). This means that plants allocate more carbon to aboveground tissue and relatively less to their roots when nutrient availability increases. As a consequence, the shoot-root ratios of N

fertilised plants increase and thus their evaporative demands (Gordon et al., 1999; Meyer-Grünefeldt et al., 2015; Dzedek et al., 2017). This in turn affects the plants’ water status and may increase their drought sensitivity. Höglberg et al. (1993) found that N additions to an initially N-limited forest increased foliage biomass and hence the trees’ water demands and the probability of water stress (e.g. indicated by an accompanying increase of leaf tissue $\delta^{13}\text{C}$ signatures). (ii) N fertilisation may affect the mortality of the trees’ fine-roots. Several studies have reported that both tree root mortality and turn-over increase as a result of high N availability or airborne N deposition (Hendricks et al., 2000; Nadelhoffer, 2000). This response could be related to the finding that N availability

affects the trees' root morphology. For example, N fertilisation can reduce the diameter of fine roots (Sun et al., 2010; Noguchi et al., 2013), making them more prone to drought stress. Increased root mortality in N fertilised environments thus could contribute to decreasing TRW during periods of drought and heat waves. (iii) N fertilisation also has the potential to decrease mycorrhiza colonization of tree roots (Sun et al., 2010; Teste et al., 2012), which could impair both the nutrient and water supply of trees and thus their vitality and stress sensitivity (Yang et al., 2014).

In contrast to mature stands, increasing N deposition and T_{mean} mutually improved RWI of young stands (synergistic effect). We hypothesise that age-related N deposition-climate interactions are attributable to shifting N demands of trees with aging. Wernsdörfer et al. (2014) have demonstrated a reverse-J-shaped relationship between wood and bark nutrient concentrations and stem diameter, indicating a decreasing (relative) nutrient demand with increasing tree age. Age-effects could also be related to competition effects in stands, since the tree density in young stands was about four times higher than in mature stands (Table 1). This suggests a higher intraspecific competition in young stands, resulting in higher belowground competition for resources such as nutrients or water. As a consequence, N demands in young stands could be higher than in mature stands, and increasing N deposition could alleviate N shortage in young stands (Högborg et al., 1993). This interpretation is supported by our data on the stand growth characteristics (Table 1), according to which young stands were less sensitive to environmental shifts than mature stands (i.e. RWI was less sensitive to climatic variables and more likely affected by other variables such as nutrient availability), indicated by the significantly lower mean sensitivity of young stands.

4.2. Interaction effects of N deposition and P_{gs}

Increased summer precipitation promoted radial increment across stands (indicated by positive estimates for P_{gs} ; Table 2), and interacted with N deposition for mature stands (negative estimate, marginal significance). The corresponding contour plot (Fig. 2 b) indicates that the negative effects of decreasing P_{gs} (with N inputs below $8 \text{ kg ha}^{-1} \text{ yr}^{-1}$) could be compensated for under high N loads (above $12 \text{ kg ha}^{-1} \text{ yr}^{-1}$). A conceivable mechanism explaining this finding could be that decreasing P_{gs} limits the trees' nutrient and thus N supply. Dannenmann et al. (2016) found that reduced soil water availability promotes N limitation of European beech due to impaired microbial N cycling. This mechanism applies to Regosol or Luvisol sites in particular, which are characterised by low water holding capacity and therefore are sensitive to desiccation (Härdtle et al., 2013). Under low P_{gs} , increasing N deposition could then compensate for N shortage caused by reduced microbial activity (Dannenmann et al., 2016).

5. Conclusions

Our findings suggest that interactions between N deposition and climatic variables are complex and have the potential to impair growth and performance of European beech. The interplay of global change drivers might cause both additive and non-additive responses, with the latter being synergistic (amplifying) or antagonistic (dampening). Estimates of tree growth responses to global change thus remain challenging, and could be further complicated due to age-, site- or species-specific responses.

Our results also indicate that interaction processes of co-occurring global change drivers could mediate N deposition effects on forest carbon sequestration. In the case of young stands, synergistic effects of warming and N deposition suggest an enhanced carbon fixation of trees. In mature stands, by contrast, the

forests' potential to sequester carbon might decrease due to antagonistic effects of warming and N deposition. This in turn emphasises the importance of multiple-factor approaches to support models aimed at improved projections of tree growth responses to global change.

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